NIMBACINUS DICKSONI, A PLESIOMORPHIC THYLACINE (MARSUPIALIA: THYLACINIDAE) FROM TERTIARY DEPOSITS OF QUEENSLAND AND THE NORTHERN TERRITORY

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A new Tertiary thylacinid, *Nimbacinus dicksoni*, shows features unique to the Thylacinidae, while retaining many other features that are plesiomorphic within the group. *Nimbacinus dicksoni* expands the diversity of the family to two genera and three species and extends its history to the Late Oligocene or Early Miocene. *Nimbacinus dicksoni* provides support for the monophyly of a group combining the Thylacinidae and Dasyuridae but suggests that these two families diverged before the Late Oligocene.

☐ *Nimbacinus dicksoni, Marsupialia, Thylacinidae, Riversleigh, Oligocene, Miocene.*

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The Thylacinidae is a family of dasyuroids known to contain only one modern species, *Thylacinus cynocephalus*, and one extinct species, *T. potens. Thylacinus potens,* from the Late Miocene Alcoota Local Fauna (Woodburne, 1967), provides little insight into the history of the group because in many respects it is almost as specialised morphologically as the modern *T. cynocephalus* (Woodburne, 1967; Archer, 1982b).

A new thylacinid from the older Tertiary deposits of Riversleigh (Queensland) and Bullock Creek (Northern Territory) is described here. It is the oldest and most plesiomorphic thylacinid known and as such encourages a re-evaluation of thylacinid phylogeny. Dental nomenclature follows Archer (1978, 1982b).

Institutional abbreviations: NTM, Northern Territory Museum; QM, Queensland Museum; AR, Archer Collection, University of New South Wales.

SYSTEMATICS

Family THYLACINIDAE Bonaparte, 1838

Nimbacinus n. gen.

TYPE AND ONLY SPECIES

Nimbacinus dicksoni n. gen. and n. sp.

GENERIC DIAGNOSIS

Nimbacinus differs from all other thylacinids in the following combination of features: 1, extremely small metaconids on all lower molars; 2, an unreduced stylar shelf region with prominent stylar cusps B and D as well as smaller cusps C and E on M^2 and M^3; 3, protoconule and metaconule present on M^2-M^4 and prominent on M^3 and M^4; 4, prominent protocristae and talonid basin ridges. *Nimbacinus* differs from plesiomorphic dasyurids (e.g. species of *Murexia*) in possessing: 1, much smaller metaconids; 2, much smaller paracones; 3, smaller stylar cusps B and E; 4, greater degree of ectoflexus on M^4; 5, smaller entoconids; 6, smaller talonid basins and protocones; and 7, longer postmetacristae and paracristids.

ETYMOLOGY

Nimba is a Wanyi Aboriginal word from the Riversleigh area meaning "little" (G. Breen, pers. comm.); *cinus* is from the Greek *kyon* meaning "dog" in reference to the dog-like shape of thylacinids. The gender is masculine.

Nimbacinus dicksoni n. sp.

HOLOTYPE

QMF16802 (formerly AR6670) a left M_2 collected in 1984 by M. Archer, H. Godthelp and S. Hand; chosen as the holotype because it is the only tooth represented in all isolated thylacinid populations from Riversleigh and Bullock Creek.

TYPE LOCALITY

Henk's Hollow Site, the Gag Plateau, Riversleigh Station, NW Queensland; Henk's

Hollow Local Fauna, Middle to Early Late Miocene (Archer *et al.*, 1989).

PARATYPES

QMF16803 (AR7852), a right maxillary fragment with P^3, M^2-M^4; QMF16804 (AR5568), a right maxillary fragment with M^2-M^4; QMF16805 (AR4056), an M^4; QMF16806 (AR9041), an M^4; QMF16807 (AR7712), an M^5; QMF16809 (AR1834), a broken right M_3, and Northern Territory Museum fossil collection number NTMP85553-3, a right dentary fragment containing P_1, P_2 and M_2.

PARATYPE LOCALITIES

All Riversleigh paratypes are from the type locality — except QMF16809 which is from D-Site, Riversleigh Station, NW Queensland (Riversleigh Local Fauna), Late Oligocene, Early Miocene, P85553-3 is from Bullock Creek, Camfield Station, Northern Territory (Bullock Creek Local Fauna).

SPECIFIC DIAGNOSIS

As for genus.

AGE, STRATIGRAPHY AND LOCAL FAUNA

The Henk's Hollow Local Fauna (Hand, 1985) is Middle to Early Late Miocene in age (Archer *et al.*, (1989). It was recovered from an unnamed freshwater limestone apparently overlying the Carl Creek Limestone which contains the Riversleigh Local Fauna (Tedford, 1967). Age estimation is based in part on the occurrence, in the Henk's Hollow Local Fauna, of a species of *Litokoala*, a phascolarctid genus otherwise known only from the Kutjamarpu Local Fauna (Woodburne *et al.*, 1985). The age of the central Australian local faunas is in doubt. Although the Ditjimanka and Etadunna local faunas have most commonly been regarded as Middle Miocene in age (Woodburne *et al.*, 1985), there are now reasons to conclude that they may be Late Oligocene (M. Lindsay, pers. comm.; Archer *et al.*, 1989, 1990; Flannery, 1990). The Kutjamarpu Local Fauna, which has been regarded to be Middle Miocene in age (Woodburne *et al.*, 1985), is more reasonably regarded as Late Oligocene to Early Miocene. On this basis, the faunal similarities between the Riversleigh Local Fauna (the oldest mammal-bearing fauna from the Riversleigh region and source of paratype QMF16809) and the Kutjamarpu Local Fauna suggest a comparable Late Oligocene to Early Miocene age for the Riversleigh Local Fauna. The Henk's Hollow Local Fauna (the type locality of *Nimbacinus dicksoni)*, as currently understood, is younger than the Riversleigh Local Fauna, but how much so is unclear. Based on the apparent absence in this Local Fauna of wynyardiids, ilariids, the rarity of balungamayine macropodoids and the abundance of balbarine kangaroos combined with the stratigraphic proximity to the Jaw Junction Local Fauna (which contains an unnamed zygomaturine similar to *Kolopsis*, a genus otherwise only known from relatively derived Late Miocene species), the Henk's Hollow Local Fauna is probably between Middle to Early Late Miocene in age. The age of the Bullock Creek Local Fauna (source of NTM P85553-3) is also uncertain but, on the basis of biocorrelation (the presence of a species of *Neohelos*, a plesiomorphic species of *Wakaleo* and the absence of wynyardiids, ilariids and other groups characteristic of the older Riversleigh mammal-rich assemblages) it also probably is Middle to Early Late Miocene in age.

DESCRIPTION

The lower molars from the Henk's Hollow samples are represented by a left M_2, QMF16802 (Fig. 1). (Paratypes QMF16809 and P85553-3 also include lower molars, but these are described and discussed separately). QMF16802 crown roughly rectilinear with anterior portion slightly narrowed. Roots of equal width. Protoconid largest cusp, followed (in decreasing order) by hypoconid, paraconid, hypoconulid, entoconid and metaconid. Metaconid positioned postero-lingual to protoconid. Paracristid longest crest followed (in decreasing order) by posthypocristid, metacristid, cristid obliqua, preentocristid and postentocristid. Crests all relatively straight. Straight lingual face on crown with small bulge around anterior end of paraconid. Posterior crown surface straight with relatively small bulge protruding posteriorly as hypoconulid. Buccal flank has posterior bulge extending from base of protoconid around crown meeting midway at posterior bulge of hypoconulid. Flanks of talonid basin converge low in centre of basin. Basin width extends slightly beyond metaconid and slightly beyond protoconid.

Maxilla represented by QMF16804 and QMF16803. QMF16803 is more complete and is the basis for this description (Fig. 2). Maxilla preserved anteriorly to alveoli for P^2, dorsally to infraorbital canal and postero-dorsally to suture with jugal. Infraorbital canal not completely enclosed by bone and opening above M^3. Very small foramen occuring slightly anterior and ventral to infraorbital canal.

Right P^3 represented by QMF16803. Crown longer than wide, roughly triangular in occlusal

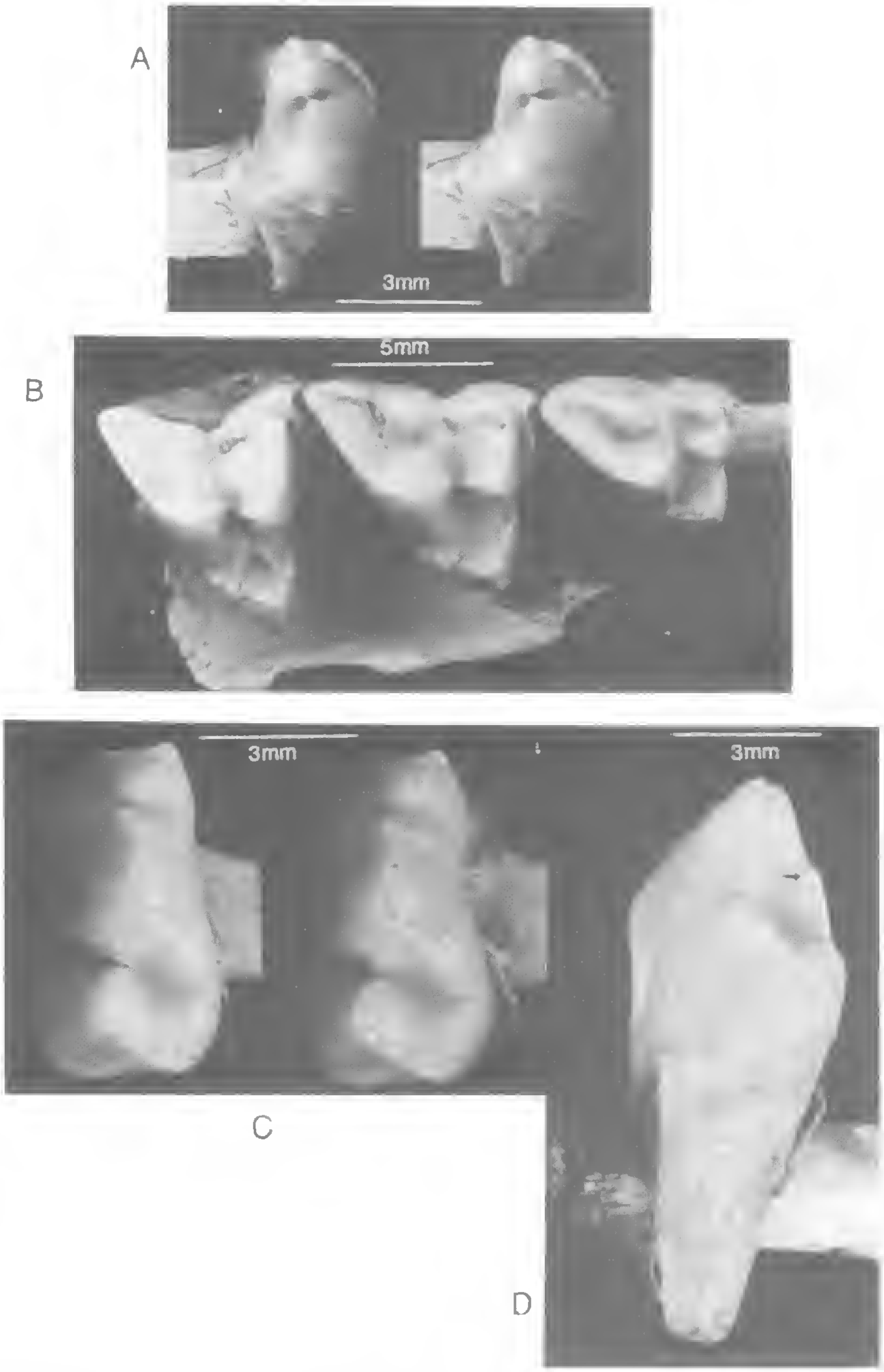

FIG. 1. *Nimbacinus dicksoni*. A, paratype QMF16809, broken right lower M_3 in occlusal view. B, paratype QMF16804, right maxillary fragment with M^2-M^4 in occlusal view. C and D, QMF16802 holotype left M_2. C, occlusal view; D, posterior view showing metaconid.

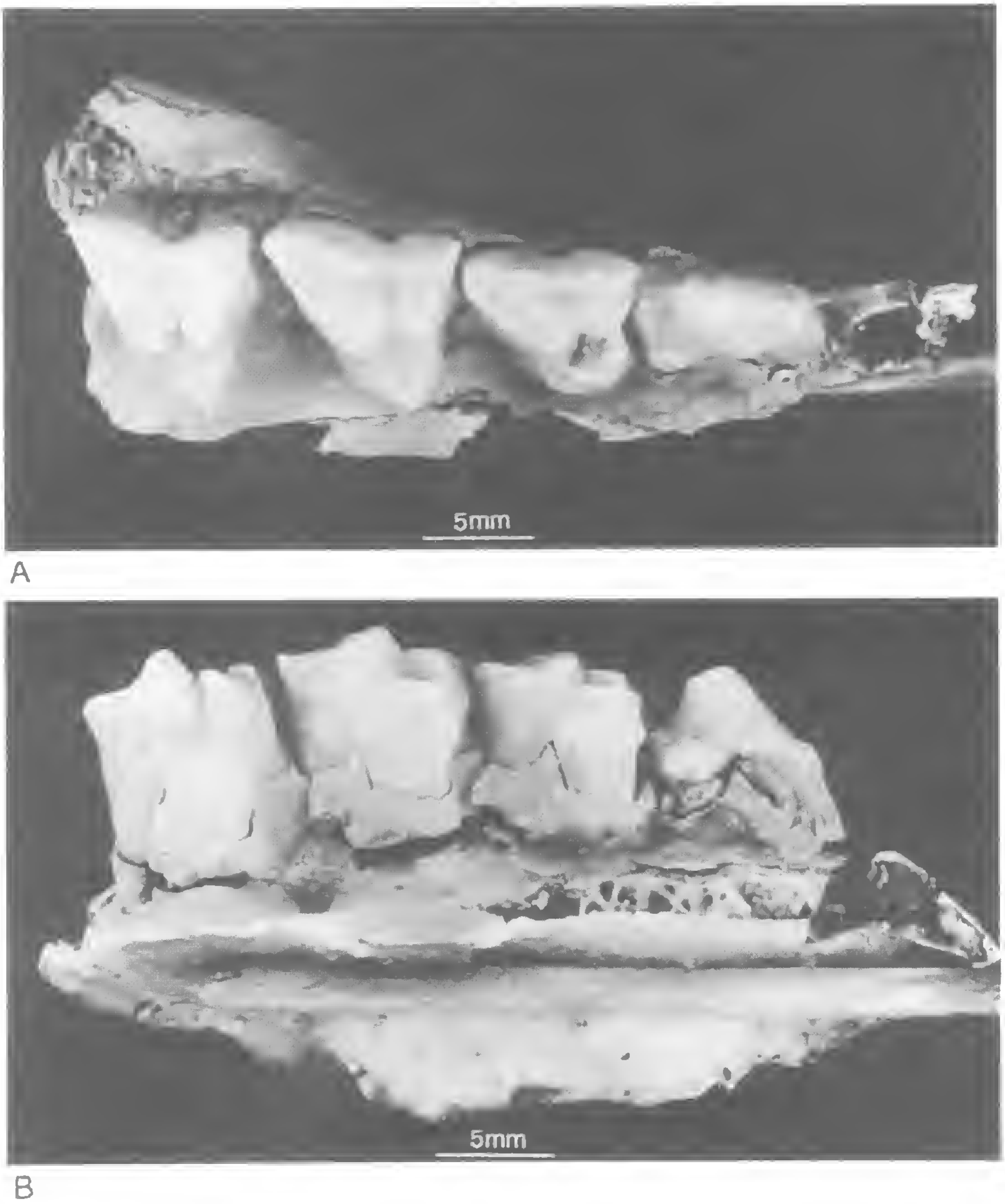

FIG. 2. *Nimbacinus dicksoni*, paratype QMF16803, right maxillary fragment. A, occlusal view; B, lingual view.

view and increasing in width posteriorly. Anterior root more massive and more nearly vertical than posterior root. Paracone medially positioned, tip worn. Tiny postero-lingual basai cuspule and posterior cuspule present. Tiny cuspule at anterior edge of crown may represent vestigial anterior cingulum. Paracone flank curved in posteriorly convex arc, continuing inclination of anterior root. Anterior surface of paracone rounded towards tip with anterior vertical crest only at base. Posterior crest extends from paracone to posterior cuspule and steeply concave in occlusal view.

M^2 represented by QMF16803 and QMF16804. Description here based on QMF16804 because this specimen is less worn. Three roots of M^2 much thinner than roots of P^3 and equal in size to each other. Each root directed vertically from each of three corners of crown. Triangular outline of crown (in occlusal view) has greatest width anteriorly. Buccal crown length exceeds anterior crown width and is exceeded by distance between protocone and metastylar corner of crown. Major cusps (in order of decreasing height) metacone, stylar cusp D, paracone, stylar cusp B, protocone. Parastylar crest present, tiny stylar cusp C in valley between stylar cusps B and D, tiny stylar cusp E on buccal edge of tooth, tiny protoconule and tiny metaconule. Small antero-buccal cingulum extends from paracone to parastylar crest. No other cingula present. Postmetacrista well-developed and longest of principal crests, followed (in decreasing length) by postprotocrista, preprotocrista, preparacrista, premetacrista and postparacrista. Major crests all meet at right angles. Postmetacrista linear, extending from metacone to metastylar corner. Preparacrista convex, connecting paracone to stylar cusp B. Postparacrista and premetacrista straight, not as well-developed as postmetacrista and meet in valley between paracone and metacone. Preprotocrista and postprotocrista are straight and approximately equal in length. These meet at tip of protocone. Postprotocrista extends posteriorly to terminate at postero-lingual base of metacone and connects to metaconular ridge. Similarly preprotocrista extends anteriorly to link with protoconular ridge at lingual base of paracone. Buccal crest runs posteriorly from stylar cusp B to posterior metastylar corner. Prominent vertical ridges extend anteriorly from stylar cusp B and lingual side of protocone. Lower buccal edge of crown bulges at base of stylar cusps B and D, producing small rounded concavity (ectoflexus) adjacent to stylar cusp C and valley between paracone and metacone. Lower lingual edge of crown rounded around protocone and forms 'U' shape when viewed occlusally. Region between paracone, metacone and stylar cusps appears enamel-free thereby facilitating removal of tooth material from the leading flanks of principal buccal shearing blades.

Right M^3 represented in QMF16804 and QMF16803. Wear is most pronounced on QMF16803 and description is based primarily on QMF16804. M^3 similar to M^2 except as follows. Crown dimensions of M^3 larger, with triangular shape of crown being less equidimensional. Metacone well-developed, distinctly higher than stylar cusp D. Protoconule, metaconule and stylar cusp C much larger on M^3. Enlargement of conules results in termination of postprotocrista and preprotocrista at tips of conules rather than at base of metacone and paracone. Stylar cusp E smallest cusp present. Preprotocrista exceeds postprotocrista in length. Preparacrista longer on M^3 than on M^2. Relative size of principal crests (from longest to shortest) are postmetacrista, preparacrista, premetacrista, preprotocrista, postprotocrista and postparacrista. Junction of preparacrista to postparacrista at paracone forms acute angle. All major crests on M^3 relatively straight including preparacrista which curves convexly at termination at stylar cusp B. Ectoflexus on M^3 greater than that of M^2. Buccal bulges of stylar cusps B and D do not extend to ends of crown. Metastylar tip forms more acute angle than in M^2. Lingual edge of tooth at base of protocone more angular than in M^2 and has prominent vertical ridge producing 'V' shape on lingual flank.

Right M^4 represented in QMF16803, QMF16804 and QMF16806. Isolated left M^4 represented in QMF16805. QMF16804 and QMF16806 show least wear and description is based on these. M^4 similar to M^2-M^3 except as follows. M^4 larger than M^2 but comparable in some dimensions to M^3. Stylar cusp D not well-developed and smaller than M^3 or M^2. Paracone second largest cusp followed by stylar cusp B. Stylar cusp D shows variation in height on M^4. QMF16806 has stylar cusp D subequal to stylar cusp B; on QMF16804 (showing similar wear pattern to QMF16806) stylar cusp D is smaller than stylar cusp C and metastylar crest. No stylar cusp E present on M^4. Paraconule and metaconule larger than on M^2 and subequal to M^3. Postmetacrista longest of crests followed (in order of decreasing length) by preparacrista, postprotocrista, preprotocrista, postparacrista and premetacrista. Junctions of these crests form sharper angles than on M^2. No buccal crest on stylar shelf region, which is reduced to greater degree. Lingual vertical ridge from protocone sharply pronounced. Lingual surface of tooth 'V'-shaped rather than 'U'-shaped as in M^2. Buccal surface of M^4 shows marked difference from that surface on M^2. Ectoflexus strongly developed. Bulges at base of stylar cusps B and D on M^2 reduced on M^4 and concavity between these enlarged and extended to anterior and posterior corners of crown. Buccal surface forms a broad 'V'-shaped concavity.

M^5 represented by isolated right tooth, QMF16807. Crown broken and similar to M^2, M^3 and M^4 except as follows. Occlusal shape of crown roughly linear with metastylar region reduced. Most prominent cusp is paracone from which extends straight preparacristid to parastylar crest at antero-buccal edge of crown. Postparacrista shorter than preparacrista and extends posteriorly to reduced metacone. Crests make wide angle at junction on the paracone. Protocone present but metaconule and protoconule reduced. No stylar shelf present. Occlusal surface at postero-buccal end of crown falls from crests after concave slope.

Meristic gradients from M^2 to M^4: postmetacristae length increases posteriorly; preparacristae length increases posteriorly; premetacristae length decreases posteriorly; lingual surface and junction between preprotocristae and postprotocristae becomes sharper posteriorly; degree of ectoflexus increases posteriorly; buccal crown length increases from M^2 to M^3, then decreases to M^4.

THE BULLOCK CREEK SPECIMEN

Specimen NTMP85553-3 is a right dentary fragment preserving a region extending from P_1 to M_2. Mental foramen occurs under diastema between P_1 and P_2. A larger foramen occurs under anterior alveoli of P_3. Symphysis extends below posterior alveoli for P_3. Small (2 mm) diastema occurs between P_1 and P_2. Diastema between P_2 and alveoli for P_3 is slightly smaller. No diastema apparent between P_3 and M_2.

Crown on P_1 linear with maximum width at middle. Anterior root roughly equidimensional in cross-section and inclined posteriorly in its alveolus. Posterior root more massive than anterior root but inclined to same degree and linear in cross-section. Protoconid positioned in middle of anterior half of crown. It supports a slight anterior cristid running lengthwise from tip of protoconid.

Roots of P_2 similar to those of P_1. Crown morphology of P_2 also resembles that of P_1, differing only in following features. P_2 has triangular-shaped crown increasing in width posteriorly from protoconid. Protoconid height almost double that of same cusp on P_1 and lies in more posterior position on crown. Anterior cristid prominent, and posterior cristid also present. Posterior half of crown does not flatten to same degree as in P_1 because of increased height of protoconid and more posterior position. In centre of posterior edge of crown is minute cuspid.

Two broken alveoli represent P_3. Size and position of these suggest a tooth similar in size to P_2.

Crown size and general morphology of M_2 resembles that of QMF16802 from Henk's Hollow sample. The following description concentrates on features that differ between the two samples.

Bullock Creek M_2 very worn. Postero-lingual surface has slightly better-developed shelf with corner of crown extending out at sharper angle than in Henk's Hollow specimen; therefore posterior width of Bullock Creek tooth slightly greater. Antero-lingual surface of Bullock Creek crown has circular curvature. Bullock Creek specimen has greater anterior thickness than Henk's Hollow specimen which thins anteriorly to greater degree.

COMPARISON OF SAMPLES

HENKS HOLLOW MATERIAL

Material representing *Nimbacinus dicksoni* from the Henk's Hollow Local Fauna includes the holotype QMF16802, and paratypes QMF16803, QMF16804, QMF16805, QMF16806 and QMF16807. These are presumed to represent a single taxon for the following reasons. QMF16803 and QMF16804 are both right maxillary fragments containing M^2, M^3 and M^4 and are very similar in size and morphology. The only significant difference between the two specimens is the degree of wear. QMF16806 and QMF16805 are isolated molars but they are virtually identical to the M^4 of QMF16803 and QMF16804. QMF16807 is an isolated M^5. No other thylacinid M^5 has been recovered from the Henk's Hollow deposit. Size and morphology, however, support the hypothesis that QMF16807 is an M^5 of *Nimbacinus dicksoni.* QMF16802 is the holotype and hence *N. dicksoni* by designation. Size and morphology suggest that this lower left molar represents the same species as the rest of the Henk's Hollow material. No other dasyuroid of comparable size has been recovered from this deposit despite preparation of a large amount of material. QMF16802 is the only thylacinid lower molar from the Henk's Hollow sample. This tooth corresponds perfectly to the occlusal features of upper molars (from the other side, QMF16803 and QMF16804). Meristic trends in *Thylacinus cynocephalus* suggest that QMF16802 is a left M_2 for the following reasons:

1) The M_2 of *T. cynocephalus* has a very reduced, simple anterior cingulum while the M_3 and M_4 have well-developed anterior cingula with a notch for the hypoconulid of the preceding molar. The Henk's

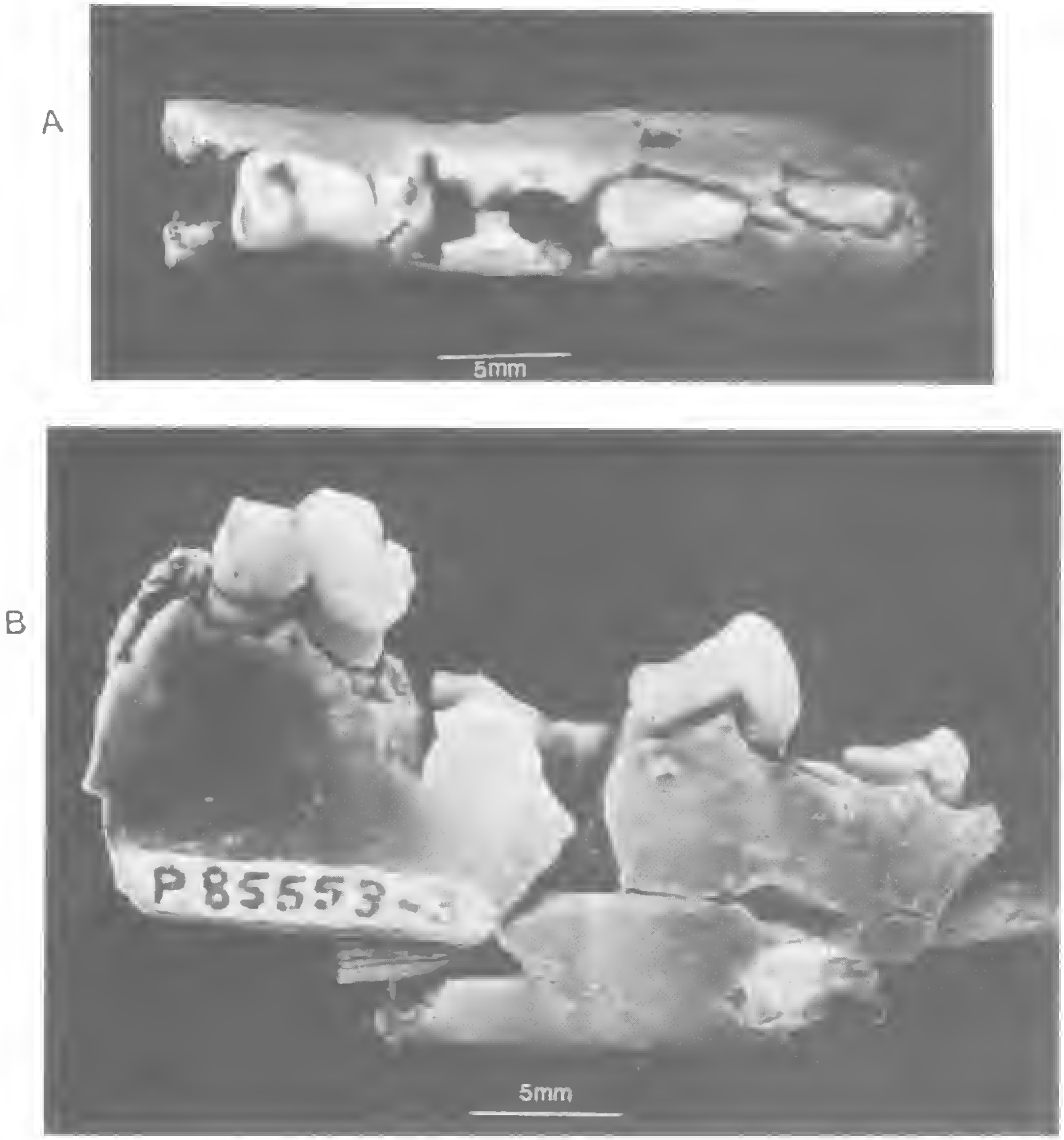

FIG. 3. *Nimbacinus dicksoni* paratype P85553-3. Right dentary fragment; A, occlusal view; B, buccal view.

Hollow lower molar has a proportionally larger single anterior cingulum but a much smaller and proportionately less well-developed cingulum than occurs on either the M_3 or M_4 of *T. cynocephalus.*

2) In *T. cynocephalus*, the paraconid of M_2 is poorly developed when compared with the paraconid of M_3 and M_4. The Henk's Hollow tooth also exhibits a relatively poorly developed paraconid.

3) In *T. cynocephalus*, the M_2 is subequal in crown length to that of M^2. Similarly, the M_3 and M_4 correspond in size to M^3 and M^4 respectively. The M_2, however, is much smaller than M^3 or M^4. The maxillary fragments from Henk's Hollow, although from the opposite side of the mouth, permit crown length comparisons with the lower molar which is subequal in size to M^2 and much smaller than M^3 and M^4.

4) Protocone and talonid width are directly correlated because they occlude. Direct correlation could not be demonstrated because upper and lower teeth are from opposite sides, but the talonid

width of the lower molar is subequal to the protocone width of the M^2 of the maxillary fragments.

The Bullock Creek Material

Specimen NTMP85553-3 (Fig. 3) was collected by P. Murray and party from the Camfield Beds of Victoria Downs Station, Northern Territory. The faunal assemblage from this formation, known as the Bullock Creek Local Fauna (Plane & Gatehouse, 1968), has been interpreted on the basis of biochronology to be middle Miocene in age (Woodburne *et al.*, 1985). The overall morphology of the M_2 in the Bullock Creek specimen NTMP85553-3 is very similar to the holotype from Henk's Hollow, and is therefore considered to represent *Nimbacinus dicksoni*.

The Site D Specimen

QMF16809 is a right lower anterior molar fragment from the Carl Creek Limestone. It was collected by G. Clayton, S. Hand and M. Archer at Site D Locality (Tedford, 1967), Riversleigh Station. It is the anterior half of a right lower molar and is the only thylacinid material recovered from this site. Conclusions about meristic homology (as an M_2) and the specific identity of the tooth need qualification. It is equal in size to the M_2 of *Nimbacinus dicksoni* but two morphological features suggest that this tooth could not be an M_2. First, the anterior cingulum is strongly developed in the Site D molar. This produces a distinct 'V'-shape on the anterior surface of the crown, a feature found in M_3-M_5 of many marsupials as an adaptation to prevent food from lodging between adjacent molars. This feature is never found on M_2. Second, paraconid development increases posteriorly along the lower molar row in didelphids, dasyurids and thylacinids. The paraconid is typically poorly developed on M_2. The Site D molar has a very strongly developed paraconid, much larger than that seen in the Henk's Hollow or Bullock Creek specimens.

These features suggest that the Site D specimen, although comparable in size to the M_2 of the Henk's Hollow sample, must be either an M_3 or M_4. Thus the Site D specimen, which displays an extremely reduced metaconid for a posterior molar (a unique feature of thylacinids) must represent a smaller individual than those represented by the teeth from the Henk's Hollow and Bullock Creek samples. This is, therefore, also reason to suspect that the Site D thylacinid might represent a different, smaller species than *Nimbacinus dicksoni*.

Three morphological differences between the Site D tooth and those from the other two samples could be interpreted as indications of specific level distinction: the relatively small metaconid size, the less well developed antero-buccal margin of the crown and smaller overall size. The first two differences are not predictable attributes of a more posteriorly situated molar in dasyurids or thylacinids although the differences could represent intraspecific variation within *N. dicksoni*, a possibility that cannot be tested until larger samples are available. The possibility that the Site D specimen is specifically distinct on the basis of its small size, however, can be examined. Variation in a total combined *N. dicksoni* sample (including the Site D specimen) may be compared with that in *Thylacinus cynocephalus*, the latter being the only thylacinid represented by large samples (Ride, 1964; Dawson, 1982). The Site D tooth is not an M_2 for reasons noted above and is therefore either an M_3, M_4 or M_5. However, the further along the tooth row (i.e., closer to M_5) the tooth is, the greater the size difference between it and samples of *N. dicksoni* because the molars of thylacinids increase in size from front to back. If we presume that it is an M_3 rather than an M_4, this increases the probability that it and the other samples of *N. dicksoni* represent a single species. In order to see if the Site D tooth (presumed here to be an M_3) and the Henk's Hollow and Bullock Creek teeth could represent a single species no more variable than *T. cynocephalus*, differences between trigonid width of the smallest M_2 and that of the largest M_3 were compared in samples of modern (Tasmanian) and Pleistocene (Wellington Caves) *T. cynocephalus*. These differences are expressed below as a function of the length of the M_2 crown in order to standardise the measure. Tooth length is taken as the greatest antero-posterior dimension of the enamel crown. Tooth width equals the transverse width across the widest part of the trigonid. Thus the ratio for each sample is: (smallest M_3 width - largest M_2 width) / M_2 length. *Nimbacinus dicksoni* (all samples plus Site D specimen): (2.85-3.18) / 6.57 = 0.05 (where 2.85 and 6.57 are the dimensions of QMF16809 and QMF16802 respectively, and 3.18 the width of the Site D trigonid). Modern *T. cynocephalus*: (5.03-4.95) / 2.91 = 0.01 (where 5.03 and 4.95 represent AR8409 and S789 respectively and 9.21 represents S789). Pleistocene plus modern populations of *T. cynocephalus*: (5.03-6.23) / 12.53 = 0.10 (where 5.03 and 12.53 represent AR8409 and MF308 respectively and 6.23

represents MF308); (for specimen details see Appendix).

It can be seen that the combined range of the *Nimbacinus dicksoni* sample (with the Site D tooth included) exceeds that of modern *T. cynocephalus*. However, the size range ratio of *T. cynocephalus* when Pleistocene and modern samples (the two being regarded to represent *T. cynocephalus* by Ride, 1964 and Dawson, 1982) are combined is 0.10. This value is higher than that for the modern specimens alone and exceeds that for the combined *N. dicksoni* sample. Thus on the basis of size alone, the Site D tooth cannot be excluded from *N. dicksoni*. This tooth may, however, represent a smaller population of the species than that which occurred in the Henks Hollow and Bullock Creek deposits. As is evident from these calculations, the same magnitude of size difference exits between modern plus Pleistocene samples of *T. cynocephalus*.

CHARACTER ANALYSIS

Phylogenetic systematic methodology was used to examine the relationships of *Nimbacinus dicksoni* within the Thylacinidae. This analysis used the method of out-group comparison elaborated by Watrous and Wheeler (1981) in order to determine character state polarities within the Thylacinidae. Richardson, Baverstock and Adams (1986) suggest that the out-group should consist of several species which are distantly related yet as close as possible to the group under study. Dasyurids have been determined to be the most appropriate out-group on the basis of morphological, serological and other studies of thylacinid and dasyurid relationships (e.g. Simpson, 1941, 1945; Marshall, 1977; Archer, 1982a; Szalay, 1982; Sarich *et al.*, 1982). Of the dasyurids, the relatively most plesiomorphic and unspecialised species of *Murexia* were interpreted (*fide* Archer, 1976) to represent the plesiomorphic states of polymorphic characters within the Dasyuridae.

CHARACTERS CONSIDERED AND THEIR CHARACTER-STATE POLARITIES

1. Paracone Height: In the oldest and most plesiomorphic marsupials (e.g. species of the genera *Alphadon*, *Pediomys* and *Didelphodon*), the paracone is lower than the metacone, a condition that appears to represent an autapomorphic feature of marsupials. Some dasyurids, most borhyaenoids, sparassocynids and thylacinids, however, show further reductions of paracone height considered to be apomorphic within the Marsupialia (Archer, 1982a). Of thylacinids, *T. cynocephalus* exhibits extreme paracone reduction while *T. potens* shows less but still marked reduction of the paracone. In *Nimbacinus dicksoni*, the height of the paracone relative to the metacone is slightly lower than that for most dasyurids and therefore represents an apparently plesiomorphic state within the Thylacinidae.

2. Stylar Cusp B: Stylar cusp B is present and large in almost all plesiomorphic marsupials. This appears to be the plesiomorphic state among dasyuroids being present in, for example, species of *Murexia*. In dasyurids, loss of stylar cusp B from M^2 is a synapomorphy of several morphologically specialised lineages such as the dasyurines (Archer, 1976). In *Thylacinus cynocephalus* stylar cusp B is extremely reduced on M^2 and minute on M^3 and M^4 (Archer, 1976). In *Thylacinus potens*, there is a similar reduction of stylar cusp B on M^4 but its condition is indeterminate on the other molars because of poor preservation. Stylar cusp B in *N. dicksoni* is also reduced although not to the same degree as in species of *Thylacinus*. Stylar cusp B is small on M^2 but prominent on M^3 and M^4. On M^4 it is the third largest cusp on the crown. In this condition *N. dicksoni* displays a more plesiomorphic condition than the species of *Thylacinus*.

3. Stylar Cusp C: Some Caenozoic didelphids exhibit a reduction of stylar cusp C in contrast to the condition of peradectids. A small stylar cusp C has been considered to be plesiomorphic within the Marsupialia (e.g. Archer, 1976). *Thylacinus cynocephalus* shows no sign of stylar cusp C on any molars. *T. potens* shows a small stylar cusp C on M^4. The preservation of M^2 and M^3 of *T. potens* is too poor to determine the size of this cusp on these teeth. In *N. dicksoni* stylar cusp C is minute on M^2 and slightly larger on M^3 and M^4. On M^4 it is comparable in size to stylar cusp D (which is relatively more prominent on M^2 and M^3). Stylar cusp C on the M^4 of *N. dicksoni* is relatively larger than that seen on M^4 of *T. potens*. This suggests that, in this regard, *N. dicksoni* displays a more plesiomorphic condition than any other thylacinid.

4. Stylar Cusp D: Stylar cusp D is present in didelphids and dasyurids. In dasyurids this cusp tends to be largest on M^2 and M^3 (Archer, 1976). *Thylacinus cynocephalus* has lost this cusp on all molars. *T. potens* shows a reduced stylar cusp D on M^4 which is larger in height than stylar cusp C. The damaged M^3 of *T. potens* suggests a better-developed stylar cusp D than that on M^4.

Stylar cusp D on the M^4 of *Nimbacinus dicksoni* is only slightly larger than that seen in *T. potens*. However, on the M^2 and M^3 of *N. dicksoni*, stylar cusp D is very large and comparable to that of dasyurids. This condition in *N. dicksoni* is therefore interpreted to represent a more plesiomorphic condition while the reduced state of stylar cusp D in other thylacines is interpreted as the apomorphic condition.

5. Stylar Cusp E: Stylar cusp E is present in some peradectids and many dasyurids (Archer, 1976). *Thylacinus cynocephalus* has a small cusp in the position of stylar cusp E on M^2 and M^3 and is the largest of the cusps present. No stylar cusp E occurs on M^4. Stylar cusp E does not occur on any of the molars of *T. potens*. Specimen QMF16804 of *N. dicksoni* exhibits very little wear and reveals a vestigial stylar cusp E on M^2 and M^3. No stylar cusp E is present on M^4 of this species. Reduction of stylar cusp E is considered an apomorphic condition within the Thylacinidae but the complete loss of this cusp in *T. potens* appears to represent an autapomorphic condition.

6. Protoconules: Almost all Cretaceous peradectids display protoconules and metaconules. These are also present in most didelphids and many dasyurids. The presence of these cuspules is therefore considered to be plesiomorphic and their reduction or loss apomorphic.

In dasyurids, if a protoconule is present a metaconule is usually also present. In rare cases a protoconule is present without the simultaneous presence of a metaconule (e.g. *Thylacinus potens*). The opposite is also seen to occur. A very reduced metaconule may be present without the presence of a protoconule. Clearly the two conditions can vary independently and should be analysed separately.

Thylacinus cynocephalus lacks the protoconule on all molars. The presence of a protoconule on the M^2 of *T. potens* is indeterminate. The M^4 of *T. potens* appears to have a reduced protoconule. *Nimbacinus dicksoni*, in contrast, has a large and distinct protoconule on M^3 and M^4. The M^2 has an extremely small protoconule, a common condition for the M^2 of dasyurids. *N. dicksoni* thus appears to display the plesiomorphic condition while *T. potens* and *T. cynocephalus* exhibit apomorphic states.

7. Metaconules: The metaconule is present in all Cretaceous peradectids, most didelphids and many dasyurids. The presence of a well-developed metaconule is considered plesiomorphic and the loss or reduction of this cusp apomorphic. Metaconules are absent on the teeth of *T. cynocephalus*. Similarly, *T. potens* has no distinguishable metaconules on any molar. *Thylacinus potens* therefore displays the variable loss of one conule without loss of the other. *Nimbacinus dicksoni* has a large and distinct metaconule on M^3 and M^4 but not on M^2. It therefore exhibits a relatively plesiomorphic condition while *T. potens* and *T. cynocephalus* display an apomorphic condition.

8. Pre- and Postprotocristae: Presence of distinct preprotocristae and postprotocristae occurs in peradectids, most didelphids and plesiomorphic dasyurids and is therefore considered to be the plesiomorphic state within dasyuroids. Variation in these features does not appear to be correlated with the size of the protoconules and metaconules because some dasyurids, such as species of *Phascogale*, exhibit distinct pre- and postprotocristae while the proto- and metaconules are very reduced. Reduction of the pre- and postprotocristae is an apomorphic condition in *Thylacinus cynocephalus*. Protocristae are extremely reduced on M^4 but are more evident on M^3. The M^2 shows an almost total loss of protocristae. *T. potens* shows less extreme reduction of the protocristae of M^4 in contrast to the condition seen in *T. cynocephalus*. The M^3 of *T. potens* also shows reduction of the protocristae while the condition on M^2 is unclear. *Nimbacinus dicksoni* displays the plesiomorphic condition with sharp and distinct protocristae on both M^3 and M^4. The protocristae of M^2 are slightly less pronounced.

9. Preparacristae and Postmetacristae: Archer (1982b) considered the proportional size reduction of the preparacristae to be associated with a functional complex correlated with elongation of the postmetacristae. *Thylacinus cynocephalus* shows this correlation in that the preparacristae are small relative to tooth size while the postmetacristae are extremely elongate.

The proportional size of the preparacristae in peradectids, didelphids and unspecialised dasyurids is approximately half the length of the anterior tooth surface of the M^2 and M^3 while the preparacrista of M^4 is slightly longer. This condition is considered to be the plesiomorphic state. *Nimbacinus dicksoni* and *T. potens* show the plesiomorphic state. *Thylacinus cynocephalus*, in contrast, shows relatively shorter preparacristae which are much less than half the width of the anterior tooth surface of M^2, M^3 and also M^4. This reduction in *T. cynocephalus* appears to be autapomorphic.

Elongation of the postmetacristae is an apomorphic state displayed by borhyaenids, thylacosmilids and specialised dasyurids (Archer, 1982b). *Nimbacinus dicksoni* displays the same relative size of the postmetacristae seen in primitive dasyurids such as peradectids, didelphids and species of *Murexia*. *Thylacinus potens*, however, shows apomorphic elongation of the postmetacristae. *T. cynocephalus* displays a similar but more exaggerated elongation of the postmetacristae, these crests being slightly larger than they are in *T. potens*. Thus, the two *Thylacinus* species share the apomorphic state of postmetacristae elongation.

10. Angle Between the Preparacrista and Postmetacrista: The angle made by the intersection of lines projected along the preparacrista and postmetacrista varies among dasyurids and thylacinids. This angle is markedly acute and reasonably constant throughout the peradectids, didelphids, most dasyurids and *Nimbacinus dicksoni*. This acute condition is therefore considered plesiomorphic. The two *Thylacinus* species show a proportional increase in the size of this angle. *Thylacinus potens* displays a significant increase in this angle while this feature in *T. cynocephalus* is further increased to approximately a right angle. Thus the species of *Thylacinus* display apomorphic conditions. The increase in this angle results from an antero-posterior shift in the orientation of the preparacristae and postmetacristae. This shift is particularly well-developed in *T. cynocephalus* where the molars, especially M^4, are not equidimensional in crown outline as are those of peradectids, didelphids, dasyurids and *N. dicksoni*. This suggests that in this feature *T. cynocephalus* is the most derived member of the family.

11. Ectoflexus: Well developed ectoflexus is a feature of dasyurids. The M^4 of *Nimbacinus dicksoni*, however, exhibits better-developed ectoflexus than occurs in any dasyurid. This may reflect the reduced size of stylar cusp D in *N. dicksoni*. However, complete loss of stylar cusp D in *Thylacinus cynocephalus* has not resulted in an increase in the extent of ectoflexus. *T. potens* has very pronounced ectoflexus resulting in a 'V'-shaped buccal surface. This ectoflexus is more marked than that which occurs in dasyurids and *N. dicksoni* and may, therefore, be considered autapomorphic rather than plesiomorphic although the increased ectoflexus of *N. dicksoni* and *T. potens* may constitute a synapomorphic condition.

Thylacinus cynocephalus, in contrast to dasyurids and other thylacinids, has extremely limited ectoflexus, the buccal surface of the crown being almost straight. This condition appears to be autapomorphic within this family. Thus *N. dicksoni* and *T. potens* appear to show one apomorphic state (hypertrophied ectoflexus) while *T. cynocephalus* displays another (extreme reduction of ectoflexus), both conditions contrasting with the presumed plesiomorphic state that would have more clearly resembled that seen in dasyurids.

12. Metaconid: The metaconid of peradectids, didelphids and most dasyurids is conspicuous and unreduced. All marsupial carnivores possess metaconids except most borhyaenids and thylacinids (Archer, 1982b). Metaconid reduction on M_2 occurs in three separate dasyurid lineages (Archer, 1976) but this cusp is rarely absent. Reduction and loss of the metaconid is considered to be an apomorphic state. *Thylacinus cynocephalus* has no trace of metaconid on any of its molars. Woodburne (1967) describes *T. potens* as having no metaconid. *Nimbacinus dicksoni*, however, possesses a very reduced metaconid. In this regard, *N. dicksoni* appears to represent a condition intermediate between that of dasyurids and other thylacinids.

13. Entoconid: All peradectids and almost all didelphids (an exception being, e.g. *Monodelphis dimidiata*) possess a well developed entoconid. Most dasyurids possess an entoconid, although it is absent in several otherwise apomorphic dasyurid lineages such as species of *Planigale* and *Pseudantechinus* (Archer, 1976; 1982a). Presence of a well developed entoconid is thus presumably the plesiomorphic state.

Thylacinus cynocephalus exhibits a very reduced entoconid. This is minute on M_2 and M_4. Woodburne (1967) described *T. potens* as possessing an entoconid on the M_4. Although it is probable that the entoconid also occurs on at least M_3-M_4 of *T. potens*, Woodburne (1967) made no comment about this condition.

Nimbacinus dicksoni has an extremely small entoconid on at least the M_2. The appearance of a relatively larger entoconid in *T. cynocephalus* may be the result of reduction of surrounding cristids in this species. These cristids are well developed in *N. dicksoni* and almost completely encompass the entoconid. The relative height of the entoconid from the base of the crown in *N. dicksoni* is similar to that of *T. cynocephalus*. Thus, while all three thylacinids exhibit synapomorphically reduced entoconids this cusp is more conspicuous in *T. cynocephalus* possibly because of the autapomorphic loss of adjacent cristids.

TABLE 1. Character state polarity

Character	Plesiomorphic State	Apomorphic State (see text for details)
1 Paracone height	Prominent but < metacone	A1(red.), A2(red.+), A3(red.++)
2 Stylar cusp B	Large	A2(red.), A2(red.+)
3 Stylar cusp C	Present	A1(red.), A2(lost)
4 Stylar cusp D	Large	A1(red.), A2(lost)
5 Stylar cusp E	Present	A1(red.), A2(lost)
6 Protoconule	Prominent	A1(red.), A2(lost)
7 Metconule	Prominent	A1(lost)
8 Pre- and Postprotocrista	Prominent	A1(red.), A2(red.+)
9 Preparacrista and Postmetacrista	Long and Short (resp.)	A1(red. prepara, elong. postpara) A2 (as for A1+)
10 Angle between Prepara- & Postmetacrista	Sharp, acute	A1(acute+), A2(> 90°)
11 Ectoflexus	Present	A1(enlarg.), A2(enlarg., A3(red.), A4(red.+)
12 Metaconid	Large	A1(red.), A2(lost), A1.5(red.+)
13 Entoconid	Large	A1(red.)
14 Talonid basin ridge	Large	A1(red.)
15 Talonid basin and protocone size	Large	A1(red.), A2(red.+)

Abbreviations: red. = reduced; red.+ = reduced more than red.; red.++ = reduced more than red.+; elong. = elongated; elong.+ = elongated more than elong.; enlarg. = enlarged; enlarg.+ = enlarged more than enlarg.; elarg.++ = enlarged more than enlarg.+; A1 = 1st state of apomorphy; A2 = 2nd state of apomorphy; A3 = 3rd state of apomorphy.

14. Talonid Basin Ridge: Most plesiomorphic dasyurids have a low talonid basin surrounded by cristids. *Nimbacinus dicksoni* shares this feature with dasyurids, the talonid basin being enclosed by cristids. Woodburne (1967) described a ridge on M_3 of *Thylacinus potens* that connects the hypoconulid to the hypoconid and entoconid, thereby creating an enclosed talonid basin. *Thylacinus cynocephalus* has a very flat talonid basin. The only distinct cristid that surrounds the basin is the posthypocristid. The only structure that defines the lingual edge of the basin is the tiny entoconid. The floor of the basin slopes down towards the lingual side. *Thylacinus cynocephalus* thus displays, among thylacinids, the most apomorphic condition.

15. Talonid Basin and Protocone Size: The protocone and talonid basin occlude and are correlated as a character complex. The smaller size of both is a synapomorphy of thylacinids, borhyaenoids and some dasyurids such as *Sarcophilus* (Archer, 1982b).

Nimbacinus dicksoni has a small talonid basin compared to most dasyurids. The antero-posterior length of the protocone is also slightly smaller in this species than in dasyurids. *Thylacinus cynocephalus* has even smaller talonids and protocones. Talonid basin size in *T. potens* is uncertain but the protocone is of a similar size to *T. cynocephalus*. Thus, *N. dicksoni* is more apomorphic than dasyurids but is more plesiomorphic than *T. cynocephalus* and *T. potens*.

SUMMARY OF CLADISTIC ANALYSIS AND RESULTS

Table 1 presents the characters considered above with an indication of the plesiomorphic state for each; table 2 summarizes the polarity of character states for each of the four groups analysed.

Only the distribution of potential synapomorphic states is considered because these may represent features shared in a common ancestor. Thus, character 14 (talonid basin ridge) provides no information useful for interpreting phylogenetic relationships within Thylacinidae because only one of the three thylacinid taxa

TABLE 2. Character state distribution

Character	D	d	p	c
1	P	A1	A2	A3
2	P	A1	A2	A2
3	P	P	A1	A2
4	P	P	A1	A2
5	P	A1	A2	P
6	P	P	A1	A2
7	P	P	A1	A1
8	P	P	A1	A1
9	P	P	A1	A2
10	P	P	A1	A2
11	P	A1	A2	A3
12	P	A1	A2	A2
13	P	A1	A1	A1
14	P	P	?	A1
15	P	A1	A2	A2

Characters identified by number in Table 1. Abbreviations for taxa: D = plesiomorphic dasyurid (e.g. *Murexia* spp.); d = *Nimbacinus dicksoni*; p = *Thylacinus potens*; c = *Thylacinus cynocephalus*. Abbreviations for character states: P, plesiomorphic; A1-A3, as in Table 1.

displays an undoubted apomorphic (hence autapomorphic) condition.

HYPOTHESES ABOUT THYLACINID PHYLOGENY

Figure 4 shows the twelve different dichotomous cladograms possible for the four groups considered in the analysis. Of these only trees 1 and 3 are substantiated by the distribution of synapomorphies. Tree 3 is supported by one out of fifteen characters — stylar cusp E. Tree 1 is supported by the remaining fourteen characters. These results are summarised in Table 3.

The presence of a prominent stylar cusp E (Character 5) has been considered above to represent the plesiomorphic state and its reduction or loss as apomorphic states. If correctly interpretated in terms of polarity, the condition in *Thylacinus cynocephalus* would be plesiomorphic in contrast to the condition seen in all other thylacinids. *Nimbacinus dicksoni,* which in all other characters appears to be the most primitive thylacinid, has only a vestigial stylar cusp E on M^2 and M^3; and the cusp is entirely lost in *T. potens.*

It is possible, however, that the cusp identified here as stylar cusp E in *T. cynocephalus* is incorrectly identified. Archer (1982b) considered that this cusp might in fact be stylar cusp D in an unusually posterior position. This alternative interpretation of the homology of this cusp appears to be supported by the development and occurrence of stylar cusps D and E within the Thylacinidae. If this cusp is stylar cusp D rather than E, it may represent a stage in the reduction of stylar cusp D and the enlargement of the posterior region of the teeth, a trend supported by the overall morphology of all other thylacinids.

Stylar cusp D is very well-developed on the M^2 and M^3 of dasyurids. This condition is found in *N. dicksoni* where, as in dasyurids, it is the largest of the stylar cusps. The M^4 in both cases has a relatively smaller stylar cusp D. *Thylacinus potens* appears to have a better-developed stylar cusp D on M^3 than on M^4. The better development of this cusp on M^2 and M^3 in contrast to its size on M^4 appears to be a size relationship characteristic for stylar cusp D in dasyurids. With the phylogenetic increase in development of the posterior region of the tooth in thylacinids, the stylar cusps may have shifted posteriorly and what we at first interpreted to be stylar cusp E in *Thylacinus cynocephalus* may in fact be stylar cusp D. This conclusion would remove any support for Tree 3 leaving Tree 1 as the only one to be supported by the character analysis (Fig. 5).

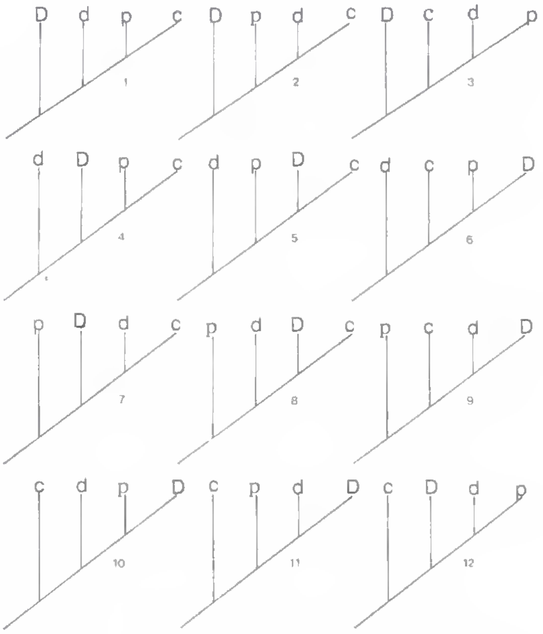

FIG. 4. Twelve possible cladograms involving dasyurids and thylacinid species. D, dasyurids (e.g. species of *Murexia*); c, *Thylacinus cynocephalus*; p, *Thylacinus potens*; d, *Nimbacinus dicksoni.*

TABLE 3.

Tree	Characters in Support	Characters Against
1	1,2,3,4,6-15	5
2	none	all
3	5	1,2,3,4,6-15
4-12	none	all

DISCUSSION

The results of the character analysis suggest that *Nimbacinus dicksoni* is more specialised than peradectids, didelphids and most dasyurids (except *Sarcophilus*) in the reduction of the paracone, stylar cusps B and E, metaconid, entoconid, protoconid and talonid basin. It is more plesiomorphic than *Thylacinus* species in which these same features are further reduced or lost. It is also more plesiomorphic than *Thylacinus* species in the lack of enlargement of the postmetacrista and the angle formed between this crest and the preparacrista. These are carnivorous adaptations that transform the shearing structures of the molars from short transverse to more elongate longitudinal blades, features well-developed in

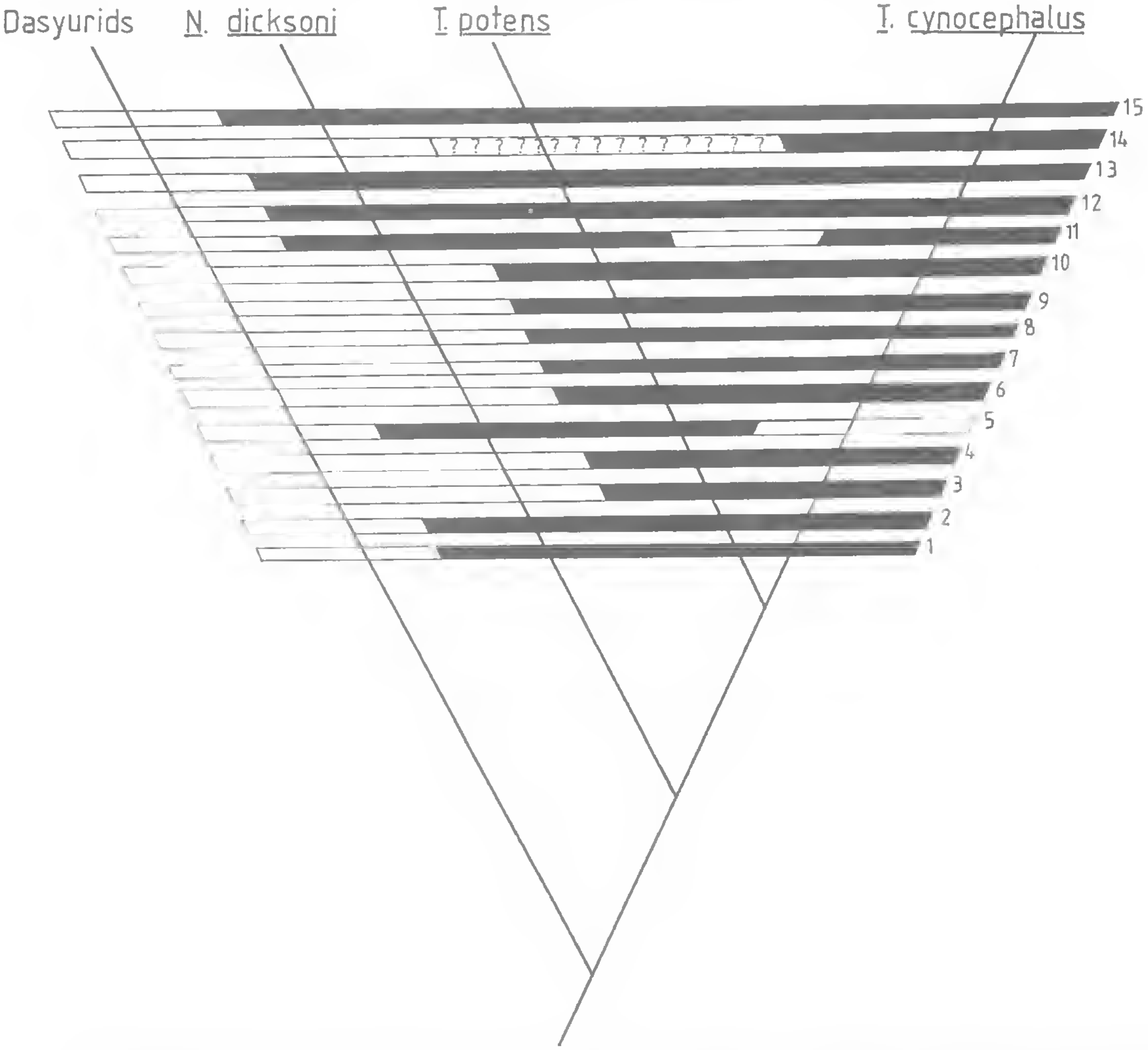

FIG. 5. The supported hypothesis of thylacinid relationships (Tree 1). Solid bar = plesiomorphic state; empty bar with question marks indicate unknown state. For character 11, there are two alternative apomorphic states (an autapomorphic condition occurring in *T. cynocephalus*; see text).

Thylacinus (among thylacinids) and *Sarcophilus* (among dasyurids).

Nimbacinus dicksoni also retains many plesiomorphic features common in peradectids, didelphids and dasyurids but which have been reduced or lost in *Thylacinus*. These are: presence of stylar cusp C; a large stylar cusp D; prominent protoconule and metaconule; prominent preprotocrista and postprotocrista; and a talonid basin ridge. Similarly, *N. dicksoni* retains a very large third premolar which is a plesiomorphic feature common in peradectids, didelphids and thylacinids but lost in all except the most plesiomorphic dasyurids (e.g. species of *Murexia)*.

Nimbacinus dicksoni shares some derived features with the more specialised carnivorous dasyurids such as *Sarcophilus harrissi* including: the reduction of the protocone; reduction of the talonid basin and its ridge; reduction of the stylar shelf region; elongation of the postmetacrista; and the increase in angle between the preparacrista and postmetacrista.

A morphocline involving progressively better-developed carnassial adaptations such as those seen in *Nimbacinus* links *Dasyurus maculatus* through *Sarcophilus moornaensis* to *S. harrissi*. This dasyurid lineage is distinct from *Nimbacinus dicksoni* in its retention of plesiomorphic features such as large metaconid and entoconid and its synapomorphic loss of P3. If *Nimbacinus dicksoni* is not part of this dasyurid radiation, the features that make it similar must have been independently acquired and thus convergent. This hypothesis is all the more probable because these are features that have been convergently developed in other marsupial groups (e.g. borhyaenoids; see Archer, 1982b).

Nimbacinus dicksoni also shares features with *Dasylurinja kokuminola* which is represented by a very small isolated right M^4 from the Late Oligocene Yanda Local Fauna, South Australia. Archer (1982a) concluded that it is a distinct dasyurid lineage unrelated to any previously known dasyurid subfamily. The features shared by both *D. kokuminola* and *Sarcophilus*, *Dasyurus* and *Satanellus* were considered by Archer (1982a) to be the result of convergence because *D. kokuminola* appears to be more autapomorphic than species of these three genera (e.g. in the extent of reduction of the metaconule, protoconule and the paracone).

Archer (1982a,b) did not consider possible relationship of *D. kokuminola* to thylacinids. It shares with thylacinids an antero-posteriorly compressed protocone, a reduced paracone and extreme enlargement of the postmetacrista. *Nimbacinus dicksoni* shares additional (presumably plesiomorphic) features with *D. kokuminola*, including the presence of stylar cusps B, D, E and possibly C, a combination of stylar cusps not found in any other dasyurid group. *Dasylurinja kokuminola*, however, shows a more extreme apomorphic state than *N. dicksoni* in its greater reduction of the metaconule and protoconule. *D. kokuminola* cannot, therefore, be an actual ancestor to *N. dicksoni* unless this condition has been secondarily acquired. Apomorphic reduction of the metaconule and protoconule is, however, also seen in species of *Thylacinus* and there is no feature of *D. kokuminola* that rules out the possibility of it being ancestral to species of *Thylacinus*. Similarly, *N. dicksoni* may be ancestral to *D. kokuminola*. However, the much larger size of *N. dicksoni* makes this hypothesis less likely.

Stirton, Tedford and Miller (1961) considered material subsequently described as *Apoktesis cuspis* from the Late Oligocene Ngapakaldi Local Fauna, to be ancestral to species of *Thylacinus*. Their conclusion was based on shared premolar size gradients which increase from P$_1$ to P$_3$ and the lack of a metaconid on M$_2$.

The premolar size gradient exhibited by *Apoktesis cuspis* is a plesiomorphic state present in unspecialised dasyurids such as species of *Murexia* (Archer, 1976, 1982a). The apomorphic reduction of the metaconid in *A. cuspis* only occurs on its M$_2$; the metaconids on its other molars are better developed. Reduction (and sometimes loss) of the metaconid on M$_2$ but large size on M$_3$-M$_5$ is common in dasyurids (e.g. some species of *Pseudantechinus*, *Dasyurus* and *Parantechinus*). Thylacinid species, in contrast, are unique in showing equivalent metaconid reduction on all molars.

Other features of *Apoktesis cuspis* noted by Stirton, Tedford and Miller (1961) do not appear to be synapomorphies with *Thylacinus* (Archer, 1976). Similarly *Nimbacinus dicksoni* shows no other features comparable to *A. cuspis*. Metaconid reduction on M$_2$ of *A. cuspis* and thylacinids is therefore concluded to be convergent.

It is possible, although less parsimonious, that *N. dicksoni* is a dasyurid lineage convergent on thylacinids. Although this would require an extreme degree of convergence, the possibility cannot be dismissed because comparable convergence has taken place between thylacinids and borhyaenids (e.g. Archer, 1982b).

Nimbacinus dicksoni is placed in the family Thylacinidae because it shows a combination of features otherwise unique to thylacinids: reduction of the metaconid on all lower molars; reduction of the stylar shelf by the independent reduction of the stylar cusps; reduction of the entoconid of the lower molars; reduction of the talonid basin and protocone; and an infraorbital canal posteriorly delimited by the jugal.

Loss of the metaconid together with the loss of the talonid basin ridge, reduction in talonid basin size and its lingual orientation places emphasis on the antero-posterior linear orientation of the cusps and crests of the lower molars. These adaptations of the lower molars are matched in the uppers by reduction of the protocone, reduction of the stylar shelf and the overall antero-posterior lengthening of the tooth. In combination these carnivorous adaptations are unique to species of *Thylacinus* and partially developed in *N. dicksoni*.

Considering phylogenetic relationships of the family Thylacinidae, *Thylacinus cynocephalus* and *T. potens* are concluded to be sister-species of a monophlyetic group rather than transformational members of an anagenetic lineage. The impropriety of considering *T. potens* as the actual ancestor of *T. cynocephalus* is indicated by the suite of autapomorphic features in *T. potens* (e.g. the enlargement of the ectoflexus) absent in *T. cynocephalus*.

So far as known, *Nimbacinus dicksoni* exhibits no feature that would prohibit it from being a direct ancestor to all species of *Thylacinus*. Similarly, no feature precludes *Dasylurinja kokuminola* from being ancestral to species of *Thylacinus*. Thus there are at least three plausible phylogenetic hypotheses involving thylacinids and *Dasylurinja*: 1, all three genera could be members of a monophyletic group in which none is the direct ancestor of any other (a trichotomy); 2, *N. dicksoni* could be a direct ancestor of *Thylacinus* with the common ancestor of this group sharing a common ancestor with *D. kokuminola*; or 3, *N. dicksoni* could be ancestral to *D. kokuminola* which in turn was ancestral to species of *Thylacinus*. The possibility of species of *Thylacinus* being ancestral to *N. dicksoni* and *D. kokuminola* is remote because of the many autapomorphic features of *Thylacinus*.

Nimbacinus dicksoni appears to represent the earliest record of the family Thylacinidae. It is a relatively unspecialised thylacinid sharing features with plesiomorphic dasyurids. Apart from *N. dicksoni*, the oldest known thylacinid is the Late Miocene *Thylacinus potens* (Woodburne, 1967).

Nimbacinus dicksoni is regarded as generically distinct from species of *Thylacinus* because the difference between it and any other species of *Thylacinus* is much greater than that exhibited between the other species of *Thylacinus* or between the species of any other dasyuroid genus.

Accepting that *N. dicksoni* is a thylacinid, the concept of the Thylacinidae must be revised as follows. Thylacinids are dasyuroids with the following unique combination of features: extreme reduction of the metaconid on all lower molars; reduction of the entoconid; reduction of the stylar shelf, especially stylar cusps B and E; reduction in the size of the talonid basin and protocone; retention of a large, unreduced P3; and posterior definition of the infraorbital canal by the jugal. Of these features, metaconid reduction on all molars is a uniquely thylacinid feature.

Thylacinids differ from myrmecobiids in many features, including the reduction of the metaconid and entoconids on all molars and the presence of a well-developed postmetacrista, molariform and tritiberculo-sectorial molars. Myrmecobiids also differ from thylacinids in their common possession of five adult molars while thylacinids retain only four.

The phylogenetic relationships of thylacinids have long been the centre of debate. Two main proposals have been: 1, thylacinids are part of the Australian radiation, having diverged from ancestral dasyurids (supported by Matthew, 1915; Simpson, 1941, 1945; Tate, 1947; Marshall, 1977; Archer, 1982b, 1984; Aplin & Archer, 1987); and 2, thylacinids share their closest ties with the South American borhyaenids (proposed by Sinclair, 1906, and supported by Scott, 1913; Gidley, 1915; Loomis, 1921; Osgood, 1921; Wood, 1924; and Archer, 1976). Bensley (1903) was uncertain, but considered that thylacinids were a "foreign" element in the Australian fauna. The oldest previously named thylacinid, the Late Miocene *Thylacinus potens*, unfortunately provides little insight into thylacinid relationships, being almost as distinct from dasyurids as is *T. cynocephalus* (Woodburne, 1967; Archer, 1982b).

A morphological study of tarsal bones by Szalay (1982) identified features that appeared to separate thylacinids from borhyaenids and to ally them with australidelphian marsupials. Serology provided further support for separation of thylacinids and borhyaenids. Sarich *et al.* (1982) examined albumin taken from dried museum specimens and concluded that the living dasyurids examined and the Thylacine shared a common ancestor approximately 7 million years ago.

The rate of evolution at the molecular level has been suggested to be relatively constant (e.g. Kimura and Ohta, 1971). For this reason albumin serology has been used to provide a molecular clock (Sarich, 1977). Error in this method for estimating divergence times may occur however, if the rate of change in proteins is not always constant (Vawter *et al.*, 1980). Richardson *et al.* (1986) discuss reasons for doubting the reliability of molecular clocks. Large measures of genetic distance give a very poor estimate of time while small distances are susceptible to varying rates of evolution due to the 'bottleneck effect' (Schmitt, 1978). Thus the molecular clock is subject to error and caution must be used in its application in phylogenetic analysis.

The 7 My date of separation for thylacinids from dasyurids proposed by Sarich *et al.* (1982) is clearly in error because: 1, *Thylacinus potens* from the late Miocene is already a highly specialised thylacinid (Woodburne, 1967); and 2, *Nimbacinus dicksoni* from sediments between Late Oligocene and Middle Miocene in age is evidently a thylacinid, albeit a relatively plesiomorphic member of the family. *Nimbacinus dicksoni* provides further support for the hypothesis that thylacinids are closely related to dasyurids in its possession of many features that appear to be intermediate between those of plesiomorphic dasyurids and species of *Thylacinus*.

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APPENDIX

Pleistocene *Thylacinus cynocephalus* dental measurements:

	Tooth Length (mm)			
Specimen Number	M/2	M/3	M/4	M/5
SAM P20451	11.0	13.2	15.8	17.6
SAM P20453	10.0	12.3	—	—
SAM P20452	10.5	13.0	15.0	—
SAM P16750	c.10.0	13.5	—	—
SAM Unregistered 1	9.6	—	14.6	16.5
SAM Unregistered 2	8.0a	—	—	13.0a
SAM Unregistered 3	8.2	—	—	—
SAM P13827	9.0	c.11.0	12.5	15.0
SAM P13728	—	12.3	14.6	17.3
SPS/ANU Unreg. 1	—	—	—	9.1
SPS/ANU MM5	—	—	11.6	13.6
SPS/ANU Unreg. 2	—	11.5	13.8	14.5
ANU/NCA/B/3	8.2	10.5	11.6	—
QMF1737	—	—	16.5	—
QMF730	10.5	13.6	14.3	16.9
AMMF413	9.2	11.3	13.3	15.5
F57929	—	—	14.51	18.16
F16550	11.14	—	16.23	18.14
F57875	—	13.38	15.21	—
F16504	—	10.97	14.69	13.57
F57857	10.05	12.47	—	—
F57857	—	—	15.34	—
MF308	12.53	15.35	—	—
F57850	10.29	—	—	—
SAM P20451	—	—	7.5	8.2
SAM P204553	4.8	—	—	—
SAM P204552	5.2	6.3	6.7	—
SAM P16750	—	6.1	—	—
SAM Unregistered 1	4.4	—	6.0	7.8
SAM Unregistered 2	—	—	—	—
SAM Unregistered 3	3.9	—	—	—
SAM P13827	4.5	5.3	5.5	7.0
SAM P13728	—	6.0	—	7.8
SPS/ANU Unreg. 1	—	—	—	—
SPS/ANU MM5	—	—	4.9	6.4
SPS/ANU Unreg. 2	—	5.5	c.5.5	7.0
ANU/NCA/B/3	4.0	5.5	6.0	—
QMF1737	—	—	7.9	—
QMF730	5.7	6.4	7.4	7.8a
AMMF413	4.4	5.6	6.9	8.1
F57929	—	—	6.91	7.28
F16550	5.15	—	7.33	7.35
F57875	—	5.89	6.46	—
F16504	—	7.07	8.40	7.43
F57846	5.86	6.03	6.63	—
F57857	—	—	7.61	—
MF308	6.23	7.30	—	—
F57850	4.88	—	—	—

All data other than F and MF numbers from Dawson (1982). (a = approximately).

(1982) for other specimen details. F and MF specimens from Australian Museum collections (a = approximately).

Nimbacinus dicksoni detail measurements:

	Lowers (mm)										
	1	2	3	4	5	6	7	8	9	10	11
QMF16802	6.57	3.75	3.18	2.70	1.66	3.04	2.79	4.81	2.26	1.84	1.01
QMF16809	—	—	2.85	2.55	1.39	2.76	—	—	—	—	—
P85553-3 P1	4.38	1.68	1.52								
P2	5.88	2.85	2.05								
M2	6.75	4.03	3.05	2.54	1.52	3.42	3.32	5.19	2.80	2.49	worn

	Uppers (mm)				
	1	2	3	4	5
QMF16803 P3	8.06	4.14			
M2	7.46	5.89	2.70	2.85	2.67
M3	8.19	7.55	3.19	4.11	3.09
M4	7.35	8.77	4.81	5.84	2.68
QMF16804 M2	6.82	5.39	2.47	3.63	2.74
M3	7.65	7.40	3.33	4.81	3.01
M4	6.82	8.28	4.15	5.09	2.23
QMF16805 M4	7.83	8.86	5.06	4.40	2.48
QMF16806 M4	7.80	7.89	3.80	4.74	3.30
QMF16807 M5	4.56	7.84	4.04	3.40	2.08

Key to dental dimensions for *Nimbacinus dicksoni* specimens:

Lowers

1 = greatest length along axis of tooth; 2 = greatest width of talonid (perpendicular to long axis); 3 = greatest width of trigonid (perpendicular to long axis); 4 = protoconid to paraconid; 5 = protoconid; 5 = protoconid to metaconid; 6 = paraconid to metaconid; 7 = hypoconid to protoconid; 8 = hypoconid to paraconid; 9 = hypoconid to metaconid; 10 = hypoconid to hypoconulid; 11 = hypoconid to entoconid.

Uppers

1 = greatest antero-posterior length; 2 = greatest width perpendicular to 1; 3 = protocone to paracone; 4 = protocone to metacone; 5 = paracone to metacone.

Modern *Thylacinus cynocephalus* dental measurements:

	Tooth Length (mm)					
	LM/2	LM/3	LM/4	RM/2	RM/3	RM/4
AR1045	10.25	12.50	14.92	10.36	12.42	15.00
AR8409	9.10	11.04	12.78	—	—	—
M217	9.80	11.91	14.41	10.00	12.26	14.25
778	9.22	11.52	13.24	9.10	11.60	13.33
767	9.54	12.21	14.34	9.10	11.82	13.91
S402	8.83	11.10	13.14	—	11.30	12.28
S1180	8.69	11.32	13.14	9.45	12.00	13.66
768	9.95	12.56	14.18	9.96	11.82	14.72
770	9.52	12.82	14.73	9.09	11.96	14.51
M822	8.76	11.56	13.40	8.81	11.40	13.54
S403	8.70	11.19	13.19	8.66	11.20	12.92
M1129	9.30	12.16	13.83	9.26	12.12	13.93
S401	11.35	12.97	14.84	11.58	12.64	15.09
775	8.59	11.32	13.75	9.22	11.29	13.84
S789	8.35	11.32	13.96	9.21	11.48	13.09
776	10.01	12.21	14.35	9.90	12.19	14.15
769	9.59	12.22	14.98	9.85	12.51	—

	Tooth Width (mm)					
	LM/2	LM/3	LM/4	RM/2	RM/3	RM/4
AR1045	4.61	5.59	6.61	4.34	5.50	6.70
AR8409	4.15	5.03	5.85	—	—	—
M217	4.42	5.74	6.52	4.48	5.54	6.55
778	3.98	5.29	6.14	4.21	5.31	6.00
767	4.61	5.76	6.61	4.66	6.00	6.76
S402	4.30	5.32	6.19	—	5.32	6.10
S1180	4.32	5.38	6.30	4.34	5.53	6.16
768	4.86	5.94	6.32	4.61	5.62	6.48
770	4.67	5.86	7.12	4.57	5.82	6.74
M822	4.12	5.32	6.14	4.29	5.32	6.07
S403	4.23	5.27	5.89	4.21	5.26	5.96
M1129	4.32	5.32	6.31	4.24	5.47	6.21
S401	4.75	6.00	7.03	4.80	5.89	6.92
775	4.15	5.34	6.01	4.10	5.50	6.00
S789	4.26	5.50	6.33	4.85	5.44	6.22
776	4.56	5.56	6.64	4.75	5.54	6.72
769	4.62	5.44	6.61	4.64	5.74	—

All specimens other than AR numbers are from the Australian Museum collection of Tasmanian *T. cynocephalus*. AR specimens from Archer's Reference collection.